

Speaker gaze increases information coupling between infant and adult brains

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When infants and adults communicate, they exchange social signals of availability and communicative intention such as eye gaze. Previous research indicates that when communication is successful, close temporal dependencies arise between adult speakers' and listeners' neural activity. However, it is not known whether similar neural contingencies exist within adult–infant dyads. Here, we used dual-electroencephalography to assess whether direct gaze increases neural coupling between adults and infants during screen-based and live interactions. In experiment 1 ($n = 17$), infants viewed videos of an adult who was singing nursery rhymes with (i) direct gaze (looking forward), (ii) indirect gaze (head and eyes averted by 20°), or (iii) direct-oblique gaze (head averted but eyes orientated forward). In experiment 2 ($n = 19$), infants viewed the same adult in a live context, singing with direct or indirect gaze. Gaze-related changes in adult–infant neural network connectivity were measured using partial directed coherence. Across both experiments, the adult had a significant (Granger) causal influence on infants' neural activity, which was stronger during direct and direct-oblique gaze relative to indirect gaze. During live interactions, infants also influenced the adult more during direct than indirect gaze. Further, infants vocalized more frequently during live direct gaze, and individual infants who vocalized longer also elicited stronger synchronization from the adult. These results demonstrate that direct gaze strengthens bidirectional adult–infant neural connectivity during communication. Thus, ostensive social signals could act to bring brains into mutual temporal alignment, creating a joint-networked state that is structured to facilitate information transfer during early communication and learning.

neural synchronization | dyadic interaction | mutual gaze | ostensive signals | intention

Temporally contingent social interactions between adults and infants play a vital role in supporting early learning across multiple domains of language, cognition, and socioemotional development (1, 2). Infants rely heavily on the temporal dynamics of facial cues such as eye contact and gaze direction to infer intention, meaning, and causality (3–5), which is unsurprising given that infants' early visual experience is heavily composed of faces (6). Of all cues, direct gaze is thought to be one of the most salient ostensive signals in human communication for conveying communicative intent (4). Gaze also acts to release and reinforce infants' own social responses such as smiling and vocalization (7, 8). From birth, infants prefer to look at pictures of faces with direct gaze over averted gaze (9). By 4 mo, direct gaze elicits a larger amplitude in the face-sensitive N170 event-related potential (ERP) relative to averted gaze (10), which suggests that gaze also enhances infants' neural processing of face-related information.

Social Synchronization Through Gaze in Communication

According to the social brain hypothesis, human brains have fundamentally evolved for group living (11). Social connectedness is created when group members act jointly (e.g., synchronously) or contingently (e.g., turn-taking) with each other (12). Even infants

show synchronization with their adult caregivers, and adult–infant temporal contingencies have long been observed in behavioral and physiological domains. For example, patterns of temporally synchronous activity between parent and child during social interaction have been noted for gaze (13), vocalizations (14), affect (15), autonomic arousal (16, 17), and hormones (18). The synchronization of gaze (through mutual gaze and gaze-following) is thought to foster social connectedness between infants and adults (19). Previous research has also suggested that infants, like adults (20), show neural synchronization (or phase-locking) of cortical oscillatory activity to temporal structures in auditory signals (21). However, adult–infant behavioral and physiological synchronization is typically observed over much slower timescales (e.g., minutes or seconds) than neural synchronization (tens or hundreds of milliseconds). Thus, it remains to be seen whether neural synchronization also develops between infants and adults during social interaction and if/how such neural coupling is related to social synchronizing signals like gaze.

Recently, researchers have begun to examine the neural mechanisms that support the contingency (temporal dependency) of one partner's neural activity with respect to the other during social interactions (see refs. 22 and 23 for reviews). This work has revealed that during verbal communication (especially face-to-face communication, which permits mutual gaze), adult speaker–listener pairs develop synchronous patterns of activity between brain regions such as the inferior frontal gyrus, prefrontal, and parietal cortices

Significance

During communication, social ostensive signals (like gaze) are exchanged in a temporally contingent manner. Synchronized behavior creates social connectedness within human dyads, and even infants synchronize behaviorally with adults. However, the neural mechanisms that support infant–adult synchronization are unknown. Here, we provide evidence that infants up-regulate neural synchronization with adult partners when offered direct ostensive gaze, as compared with gaze aversion. Gaze therefore brings infant–adult neural activity into mutual alignment, creating a joint-networked state that may facilitate communicative success. Further, infants' own communicative attempts were positively associated with adults' neural synchronization to them, indicating mutual regulation of synchronization within infant–adult dyads. Thus, interpersonal neural synchronization may provide a mechanism by which infants construct their own earliest social networks.

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(24, 25). Further, the strength of speaker–listener neural synchronization predicts communication success (26). Thus, in adults, effective communication involves the mutual alignment of brain activity, as well as the temporal alignment of behavior (e.g., conversational turn-taking and mutual gaze). However, to our knowledge, no previous research has yet investigated whether infants' neural activity also shows contingency on an adult partner's neural activity and whether gaze acts as a neural synchronization cue during adult–infant communication.

Gaze-Cuing of Interpersonal Neural Synchronization

Here, we assessed whether the temporal dependency (synchronization) between adult and infant neural signals differed between direct and indirect gaze. Two experiments were performed to assess gaze-cuing of interpersonal synchronization in video and live modalities, respectively. In experiment 1, infants watched a pre-recorded video of an experimenter singing nursery rhymes. Patterns of temporal dependency were assessed between infants' neural activity recorded "live" and adult's prerecorded neural activity (Fig. 1). We manipulated the adult speaker's gaze to be either direct to the infant, indirect (head averted at a 20° angle), or direct-oblique (head averted but eyes toward the infant). The direct-oblique condition was included to control for the side view of the face that was presented during indirect gaze and to preclude the possibility that infants were responding to superficial visual differences between stimuli. In experiment 2, which used an entirely separate cohort, infants listened live to an adult reciting nursery rhymes while she presented direct or indirect gaze to the infant. Partial directed coherence (27), a statistical measure of Granger causality (28), was used to measure gaze-related changes in interpersonal neural synchronization within the adult–infant dyadic social network.

Predictions

In terms of affect and physiological changes, research has shown that the influence of infants and parents on one another is bidirectional (29, 30). Accordingly, we predicted that (i) significant neural coupling would exist between adults and infants during social interaction, (ii) direct (and direct-oblique) gaze would both be associated with higher interpersonal neural connectivity than indirect gaze, and (iii) in experiment 1 (video), only unidirectional [adult-to-infant ($A \rightarrow I$)] coupling would be observed, but in experiment 2 (live), bidirectional [adult-to-infant ($A \rightarrow I$) and infant-to-adult ($I \rightarrow A$)] coupling would be observed. Further, as temporally contingent social interactions with adults are known to facilitate infants' own vocalizations (8, 31), we predicted that infants' vocalization efforts would be greater during direct than indirect gaze.

Results

Gaze Modulation of Interpersonal Neural Connectivity. General Partial Directed Coherence (GPDC) measures the degree of influence that each electrode channel directly has on every other electrode channel in the network (27). Here, GPDC values were computed for real and surrogate (shuffled) data, for all nonself channel pairs (connections), for each participant dyad, for each gaze condition, and in Theta and Alpha EEG bands (Fig. 1 *C* and *D*). In the subsequent network diagrams (Figs. 2 and 3), only connections whose GPDC values significantly exceeded their surrogate threshold are plotted. A breakdown of GPDC values for each neural connection is provided in *SI Appendix, section 1* (*SI Appendix, Tables S1 and S2*). Here we focus our analysis on mean $A \rightarrow I$ and $I \rightarrow A$ connectivity.

Experiment 1: Video. Only unidirectional $A \rightarrow I$ connectivity was observed in experiment 1; no significant $I \rightarrow A$ connectivity was detected (Fig. 2). This confirmed the validity of the GPDC measure as infants could not have affected the adult's prerecorded neural activity. Dunnett's tests revealed that, as predicted, $A \rightarrow I$ connectivity was (i) significantly stronger for direct > indirect gaze in both Theta and Alpha bands ($P < 0.01$ and $P < 0.05$, respectively, one-tailed) and (ii) significantly stronger for direct-oblique > indirect gaze in both Theta and Alpha bands ($P < 0.0001$ for both, one-tailed). However, while connectivity in the direct and direct-oblique conditions was not significantly different in the Theta band ($P = 0.30$) as predicted, for the Alpha band a significant difference between these conditions was observed (direct-oblique > direct, $P < 0.01$).

Experiment 2: Live. During the live experiment, bidirectional connectivity was observed with significant $A \rightarrow I$ as well as $I \rightarrow A$ influences (Fig. 3).

Regarding $A \rightarrow I$ connectivity, consistent with experiment 1, Dunnett's tests revealed that the adult's influence on infants was significantly stronger for direct > indirect gaze in both Theta and Alpha bands ($P < 0.05$ and $P < 0.0001$, respectively, one-tailed).

For $I \rightarrow A$ connectivity, Dunnett's tests indicated that infants' influence on the adult was likewise significantly stronger for direct > indirect gaze in both Theta and Alpha bands ($P < 0.01$ and $P < 0.05$, respectively, one-tailed).

Infant Vocalization Analysis. For experiment 1 (video), there was no difference in the number of infant vocalizations (summed over all categories) between gaze conditions (means: direct = 8.2 per infant, indirect = 7.4, direct-oblique = 7.1), $F(2, 32) = 0.29$, $P = 0.75$, $\eta_p^2 = 0.02$. There was also no difference in the duration of vocalizations across gaze conditions (means: direct = 0.69 s per

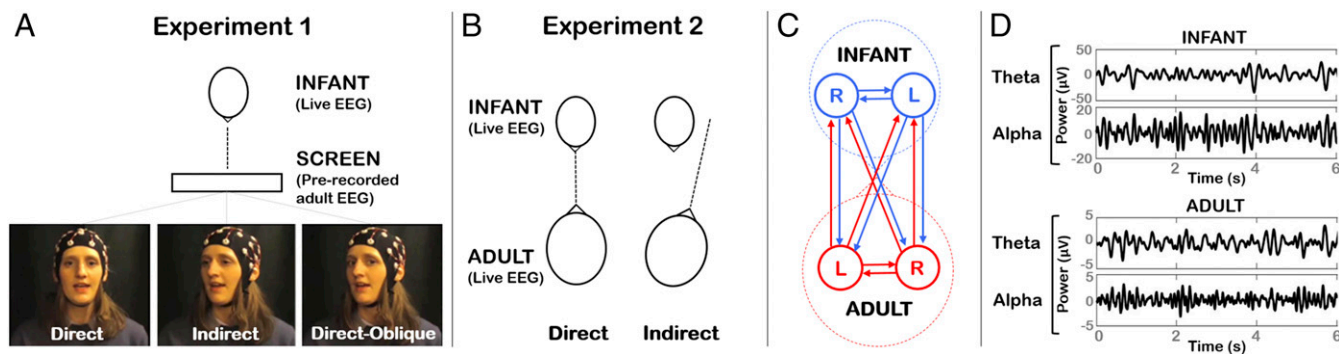


Fig. 1. Illustration of experimental protocols and connectivity analysis. (A) In experiment 1, infants viewed a video screen showing an experimenter reciting nursery rhymes. Three gaze conditions were presented interleaved: direct, indirect (head averted by 20°), and direct-oblique (head averted by 20°, direct gaze). The infant's live EEG was compared with the adult's prerecorded EEG. (B) In experiment 2, infant and adult sat opposite each other. Direct and indirect gaze (head averted by 20°) conditions were presented. (C) The adult–infant network comprised left (L) and right (R) electrodes each from the infant and adult. Interpersonal neural connectivity was assessed across all pairwise connections between electrodes using partial directed coherence. (D) Examples of infant and adult EEG data, which were analyzed within Theta (3–6 Hz) and Alpha (6–9 Hz) bands.

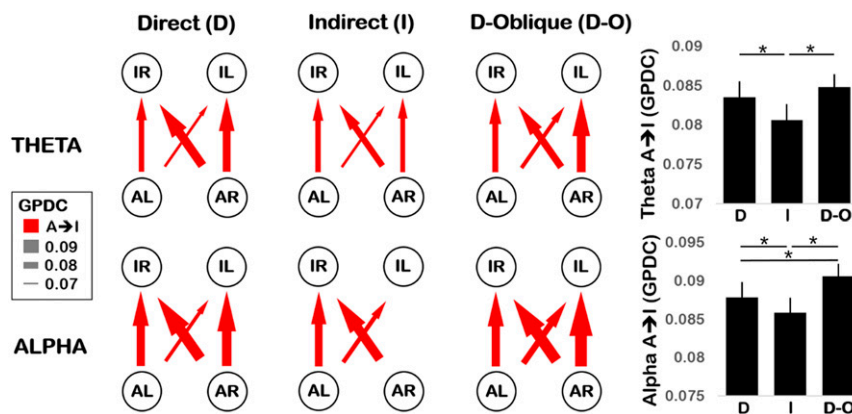


Fig. 2. (Left) Network depiction of experiment 1 Theta (3–6 Hz, Top) and Alpha (6–9 Hz, Bottom) connectivity, plotting GPDC values for direct (Left), indirect (Middle), and direct-oblique gaze (Right) conditions. Nodes represent C3 (L) and C4 (R) electrodes for adult (A) and infant (I). Arrows indicate the direction and strength of connectivity (higher GPDC value, thicker arrow). Connections that do not significantly exceed the surrogate threshold are excluded. (Right) Grand mean GPDC values averaged across all adult-to-infant (A → I) connections for Theta (Top) and Alpha (Bottom) in direct (D), indirect (I), and direct-oblique (D-O) gaze conditions. Error bars show the SEM. * $P < 0.05$.

utterance, indirect = 0.82 s, direct-oblique = 0.70 s), $F(2, 24) = 0.37$, $P = 0.70$, $\eta_p^2 = 0.03$. However, for experiment 2 (live), we observed a significantly higher number of vocalizations during direct gaze (mean 6.3 per infant) than indirect gaze (mean 5.0 per infant), $t(18) = 2.41$, $P < 0.05$, but no difference in the duration of vocalizations (mean: direct = 0.80 s per utterance, indirect = 0.85 s), $t(15) = -0.79$, $P = 0.44$.

Further, during experiment 2 (live), individual differences in infants' vocalization durations were significantly associated with their I → A GPDC values [$r = 0.67$, $P < 0.05$, Benjamini–Hochberg false discovery rate (FDR) corrected] (32) (see Fig. 4). However, this correlation only emerged during direct gaze and was absent for indirect gaze ($r = 0.07$, $P = 0.78$). Therefore, infants who produced longer vocalizations also influenced the adult more strongly—but only when she offered direct gaze. *SI Appendix, section 2* provides further analyses of infants' vocalizations.

Discussion

Temporally contingent social interactions between adults and infants scaffold early learning and development. Here, we tested the hypothesis that gaze acts as an interpersonal neural synchronization

cue between dyadic (adult–infant) partners. Two experiments were performed to assess the effect of direct speaker gaze on interpersonal synchronization using video (experiment 1) and live (experiment 2) modalities. Across both experiments, significant neural coupling between infants and adults was observed during social interaction, relative to rigorous control analyses that accounted for nonspecific neural coupling. Adult–infant neural coupling was observed consistently across video and live presentation formats, using two separate cohorts of infants. Further, during unidirectional interactions in experiment 1 (i.e., infants watching a prerecorded adult speaker), the adult had a significant influence on infants' neural activity, but (as expected) infants had no influence on the adult's neural activity. Conversely, during live (bidirectional) social interactions (experiment 2), there were significant and bidirectional patterns of influence between adult and infant.

Across both experiments, we consistently observed that direct gaze produced higher interpersonal neural synchronization than indirect gaze in both Theta and Alpha frequency bands. Further, in experiment 2 (live), the synchronizing effect of gaze was observed bidirectionally: During direct gaze, the adult had a stronger

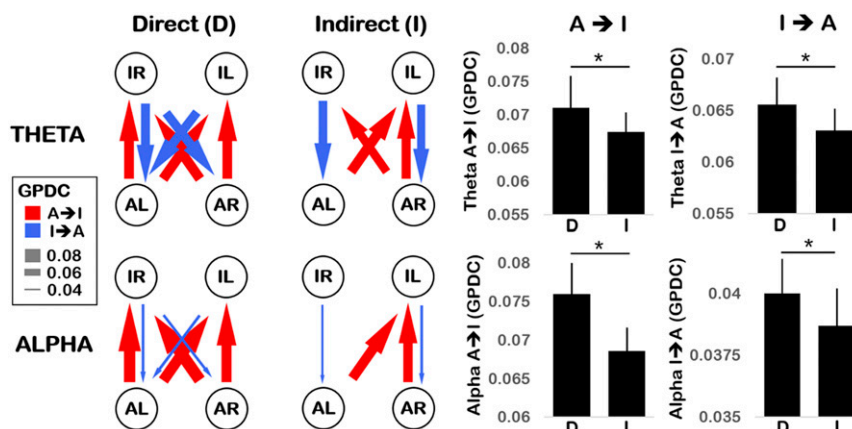


Fig. 3. (Left) Network depiction of experiment 2 Theta (3–6 Hz, Top) and Alpha (6–9 Hz, Bottom) connectivity, plotting GPDC values for direct (Left) and indirect (Right) gaze conditions. Nodes represent C3 (L) and C4 (R) electrodes for adult (A) and infant (I). Arrows indicate the direction and strength of connectivity (higher GPDC value, thicker arrow). Connections that do not significantly exceed the surrogate threshold are excluded. (Right) Grand mean GPDC values averaged across all adult-to-infant (A → I, Left) and infant-to-adult (I → A, Right) connections for Theta (Top) and Alpha (Bottom) in direct (D) and indirect (I) gaze conditions. Error bars show the SEM. * $P < 0.05$.

Methods

Participants. Experiments 1 and 2 involved separate infant cohorts—experiment 1: 19 infants (13 male, 6 female), median age 8.2 m (SE, 0.26 m), and experiment 2: 29 infants (15 male, 14 female), median age 8.3 m (SE, 0.44 m). Infants' mothers were native English speakers, and all infants had no neurological problems as assessed by maternal report. The same female adult experimenter participated in both experiments with all infants. The study received ethical approval from the Cambridge Psychology Research Ethics Committee. Parents provided written informed consent on behalf of their infants.

Materials. For both experiments, seven familiar nursery rhymes were used as sung stimuli (*SI Appendix, section 3*). Sung nursery rhymes were used because these are integral to play and caretaking routines with infants, such as during feeding and putting to sleep (38). Infants are equally or more behaviorally responsive to sung compared with spoken language (39); thus, sung speech is likely to evoke a robust neural response from infants. In experiment 1, pre-recorded video stimuli were used with mean pitch, pitch variability, duration, and loudness matched across gaze conditions (*SI Appendix, Table S5*). For experiment 2 (live), the experimenter was recorded during each session to ensure acoustic consistency across gaze conditions (*SI Appendix, Table S6*). Paired *t* tests indicated no significant differences between conditions for all acoustic parameters. The experimenter was instructed to maintain a neutral facial expression across all gaze conditions, varying only her gaze direction.

Protocol.

Experiment 1. Infants sat upright in a high chair 70 cm from a display monitor (90 cm width × 60 cm height), showing a life-sized image of a female experimenter's head against a black background. Each nursery rhyme was presented in three gaze conditions (Fig. 1): direct, indirect (head averted by 20°), and direct-oblique (head averted by 20°, but direct gaze). The direct-oblique condition was included to control for the side view of the face that was presented during indirect gaze. During stimulus recording, the experimenter gaze-fixated on a life-sized picture of an infant to standardize her visual input across conditions. Each nursery rhyme was presented six times (twice per gaze condition, order counterbalanced).

Experiment 2. Infants sat upright in a high chair facing the female experimenter at a distance of 70 cm. Each nursery rhyme was presented in two gaze conditions. In the direct condition, the experimenter looked directly at the infant while singing; in the indirect condition, she fixated at a target 20° to the left or right side of the infant (see Fig. 1 and *SI Appendix, section 4* for the experimenter's view). Each nursery rhyme was presented four times (twice direct, twice indirect, order counterbalanced).

EEG Acquisition. In experiment 1, EEG was recorded separately from infants (during testing) and from the female adult experimenter (during stimulus recording) from 32 electrodes according to the international 10–20 placement system. In experiment 2, EEG was recorded simultaneously from the infant and the adult experimenter from two central electrodes (C3 and C4), referenced to the vertex (Cz). Further details of EEG acquisition are given in *SI Appendix, section 5*.

EEG Artifact Rejection and Preprocessing. To ensure that the analyzed EEG data reflected only attentive and movement-free neural activity, a two-stage artifact rejection procedure was applied. First, session videos were manually reviewed to select only periods when infants were still and looking directly at the experimenter. Next, manual artifact rejection was performed to further exclude segments where the EEG amplitude exceeded +100 μ V. Full descriptions of the artifact rejection procedures and inclusion rates following artifact rejection are given in *SI Appendix, section 6*. Data were then downsampled to 200 Hz, low-pass filtered <45 Hz to suppress electrical line noise, and segmented into 1.0-s epochs for connectivity analysis.

EEG Analyses: Speech Artifacts, Power Spectrum, and GPDC Network Connectivity. Speech production artifacts were present in the EEG signal of the adult speaker. To assess the topography and spectral profile of these artifacts, we compared the adult's EEG during speech production relative to resting state (*SI Appendix, section 7*). Despite rigorous analyses, we were able to identify no evidence of EEG signal distortion by speech artifacts in the central region (e.g., C3/C4) in Theta and Alpha bands, although evidence of artifacts at other frequency bands and for more peripheral electrode positions was clearly present. Therefore, to avoid spurious results arising from speech artifacts, the connectivity analysis used only Theta and Alpha bands for C3 and C4 electrodes for both adult and infant. To confirm the representativeness of this region of analysis for the infant, we assessed infants' whole-head

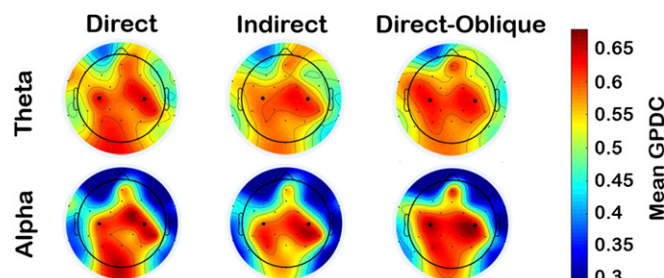


Fig. 5. Experiment 1 infant scalp topography of the mean adult (C3/C4)-to-infant GPDC values for direct gaze (Left), indirect gaze (Middle), and direct-oblique gaze (Right) conditions, for Theta (Top) and Alpha (Bottom) frequency bands. Electrodes C3 and C4 are enlarged for ease of reference. For each subplot, a top-down view of the scalp is shown where left/right map congruently to left/right sides of the infant's head, respectively.

(32-channel) connectivity to adults' C3 and C4 electrodes (Fig. 5 and *SI Appendix, section 12*). Across gaze conditions, the strongest connectivity between infant and adult was topographically observed over infants' central and posterior regions (including C3 and C4) for both Theta and Alpha bands. Therefore, C3 and C4 were indeed representative regions of analysis for the infant.

A detailed description of EEG analysis methods is given in *SI Appendix, sections 8 and 9*. Briefly, first the EEG power spectra of infant and adult signals were assessed for each experimental condition to confirm that the gaze manipulation did not generate any detectable power changes that might systematically bias the connectivity analysis. Second, to assess network connectivity in each gaze condition, GPDC—a directional causal measure of direct information flow between channels in a network—was computed (27). GPDC measures the degree of influence that channel *i* directly has on channel *j* with respect to the total influence of *i* on all channels in the network. Here, each electrode [infant left (IL), infant right (IR), adult left (AL), adult right (AR)] was one channel (Fig. 1C).

Control Analyses. The first control analysis established a threshold for non-specific connectivity between brains that was unrelated to the experimental task (*SI Appendix, section 10*). A surrogate dataset was generated for each participant pair where the fine-grained temporal correspondence between adult and infant neural signals was disrupted by randomly pairing adult and infant epochs from different timepoints within the same experimental session (i.e., shuffling). An identical connectivity analysis was then performed on this surrogate dataset. For each participant pair, neural connection, and frequency band, a threshold value was computed by taking the average surrogate value across all gaze conditions. Paired *t* tests [Benjamini–Hochberg FDR-corrected at $P < 0.05$ (32), one-tailed] were then used to assess whether the real data significantly exceeded their respective threshold values.

The second control analysis examined basic sensory processing of the speech stimulus, which could indirectly affect adult–infant neural coupling. Entrainment (oscillatory phase-locking) between the EEG signal and the speech amplitude envelope was measured in each gaze condition. As described in *SI Appendix, section 11*, no significant differences in neural entrainment to the speech signal between gaze conditions were found in either experiment.

Statistical Analysis of Gaze Effects on Interpersonal GPDC Connectivity. We hypothesized that interpersonal neural connectivity would be higher during direct (and direct-oblique) gaze than indirect gaze (i.e., direct = direct-oblique > indirect). We also wished to assess whether the adult's influence on the infant (i.e., $A \rightarrow I$ GPDC) and the infant's influence on the adult (i.e., $I \rightarrow A$ GPDC) would show the same pattern of gaze modulation. As previous work with infants has not found hemispheric differences for gaze effects (9), interhemispheric connectivity patterns were not explored further. Accordingly, the four interhemispheric connections ($L/R \rightarrow L/R$) were collapsed into one average each for $A \rightarrow I$ and $I \rightarrow A$ directional influences. These two directional indices were computed for each gaze condition, for Theta and Alpha bands. For experiment 1, only $A \rightarrow I$ connections were analyzed, as all $I \rightarrow A$ connections were not significantly above threshold (this was expected, as the adult's EEG was prerecorded).

The effects of gaze on $A \rightarrow I$ and $I \rightarrow A$ connectivity were assessed using two statistical approaches. First, to assess overall patterns and interactions, repeated-measures ANOVAs were performed, taking frequency and gaze condition as within-subjects factors. Second, to assess specific contrasts

